

THE INTERPRETATION OF THE WING VENATION  
AND TRACHEATION OF THE ODONATA  
AND AGNATHA.<sup>1</sup>

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INTRODUCTION

In 1922 Dr. A. V. Martynov read a paper before the Entomological Society of Russia on the interpretation of the veins and tracheæ in the wings of the Odonata and Agnatha (Plecoptera). His manuscript was turned over for publication in 1923 and after some delay was finally published in Russian the following year (*Rev. Russe Ent.*, 18(4):145-174). In connection with my investigations on fossil insects, I found it necessary to consult his paper, and from the very short French summary at the end of the article, I felt sure that the text contained important data and discussions which should not be overlooked. I therefore employed Miss Olga Jahr, of the Slavic Department of the Harvard Library, to assist me with the translation of the Russian. Naturally enough, Miss Jahr was unfamiliar with the biological terms, but by working together we obtained a complete English translation without much difficulty. As the translation progressed it became more and more evident that the text was fully as important

<sup>1</sup>This paper is an enlargement of the report which was read at the Russian Entomological Society, November, 1922; the manuscript was handed to the press in May, 1923.

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as I anticipated, and when the task was finished, I decided to publish the entire translation of this paper in order that it might be available to other investigators of insect phylogeny. Although there are several points on which I cannot agree with Dr. Martynov, I nevertheless consider this paper one of the outstanding contributions to insect phylogeny published during the past decade.

Dr. Martynov kindly assisted me in locating several misprints which occurred in the original text, and which had naturally caused me much confusion. The twelve figures accompanying the original article are essential for a complete understanding of the problems under discussion. Unfortunately, these figures were very poorly printed, and could not be copied for reproduction here without considerable retouching. Since there is always a possibility of distorting a figure during this process I decided that it would be better not to reprint the figures at all, but to refer the reader to the original ones. While this procedure, involving the use of two publications, may be somewhat inconvenient, I believe it introduces the lesser of two "evils."

—F. M. CARPENTER.

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Comstock and Needham published (4) their first data on the interpretation of venation of the Odonata and Agnatha in a series of articles on the wings of insects, which appeared in 1898 and 1899; and in 1903 Needham developed (10) these ideas with more details into a large work on the venation of Odonata. The interpretation of Odonate venation which was proposed in both works mentioned above was later accepted by the majority of Odonatologists and by Handlirsch (6). According to this interpretation the nervuration of the Odonata proved to be so peculiar that it could hardly be compared even with that of the Agnatha—the very closest group.

The most characteristic features of this venational system are the following: 1, the crossing of the radial sector by the bases of  $M_1$  and  $M_2$ , and its extension into the region between  $M_2$  and  $M_3$ . 2, the large size of the media, with 4 branches;  $M_1$  always leading from the base of  $M$ .

3, the curve of the cubitus (chiefly in the Anisoptera) and beyond this curve, the formation of the two branches,  $Cu_1$  and  $Cu_2$ ; formation of a triangle (or quadrilateral. 4, small size of the anal vein and its fusion with the cubitus.

It is necessary to add that according to the authors' understanding the continuation of RS to  $M_{1+2}$  is clearly a secondary vein ("bridge") and appears to be the basal part of the analogous vein indicated by Tillyard (14).

The venation of the Agnatha, as usually interpreted (Eaton, Comstock 1899, Handlirsch, Ulmer and others), is entirely different from that of the Odonata, and much more similar to that found in the more primitive Palæodictyoptera (Dictyoneuridæ). The media is simple and forks only in the distal part; RS is large and forms 4-5 branches; Cu is divided at the base, and the down curve is formed only by the lower branch; the anal veins are well developed. These differences in the interpretation of the wings of the Odonata and Agnatha are so great that the dragon-flies would on this basis be moved far off from the may-flies; but this contradicts the sum of all data in morphology and the development of these insects. If venation means anything in the explanation of phylogenetic relations of the different groups—as is unquestionably so, and the venation of the dragon-flies has been studied particularly carefully from this point of view—then either the evidence of morphology and history of development, which indicate a close relationship of the Odonata and Agnatha, are wrong; or the interpretation of the wing venation of Odonata or perhaps the Agnatha is incorrect. As the close relation between the Odonata and Agnatha is not disputed, the author began to doubt the accuracy of the usual interpretation of venation of the may-flies and partly of the dragon-flies.

It is well-known that Comstock and Needham based their interpretation of the wing venation in different groups on the study of the tracheation of the wings of nymphs and pupæ. This tracheation, it is supposed, reflects the more primitive condition of venation. The trachea RS of the Odonata (Anisoptera) turns off from R and, after crossing the bases of tracheæ  $M_1$  and  $M_2$ , enters the region between

M<sub>2</sub> and M<sub>3</sub>; tracheæ which go into these latter veins and into M<sub>1</sub> of the authors, join at the base into one common trunk, which enters the wing independently. Hence the conclusion that this trunk is M, that RS crosses M<sub>1</sub> and M<sub>2</sub>, that the bridge is a secondary formation, that the cubitus is two-branched, etc. Among the may-flies Comstock discovered at first a type of tracheation very different from that of the dragon-flies, and nearer to the normal. From this tracheation Comstock was led to an interpretation essentially similar (if not in names) to the one of Eaton (5) and other authors. Ann Morgan (8) undertook a careful investigation of the tracheation of different species of may-fly nymphs and discovered that the tracheal stem which sends small tracheæ into the branches of Comstock's RS usually arises independently from the common tracheal wing stem. Consequently, she concluded that the system of veins which include these tracheæ do not represent RS, but M, as in the Odonata. Usually in the may-flies the trachea RS does not arise from the trachea R, as it does in dragon-flies; but in one species of *Heptagenia*, and even then only in part of this specimen, Morgan succeeded in finding a weak trachea which led off from R, crossed M and entered into the region between M<sub>1</sub> and M<sub>2</sub>. Following the ontogenetic method of Comstock, Morgan concluded that the may-flies also originally had the radial sector cross the media.

Comstock, in his later work on the wings of insects (3), which represents an enlarged and somewhat changed edition of the joint work of Comstock and Needham (4), agreed with the results of Morgan and accepted, therefore, her interpretation of the wing venation of may-flies. By this interpretation the venation of the may-flies was brought (to a certain degree) up to the scheme<sup>2</sup> of the venation of the dragon-flies; but by the same interpretation the Ephemeropterid venation appeared to be extremely remote from that of the Palæodictyoptera and even the Carboniferous *Triplosobidæ* Handl. Although the latter are placed in

<sup>2</sup> Only to a certain degree, because Rs of the may-flies in Morgan's paper is not this vein in the dragon-flies. In the latter Rs (of author's) corresponds to our Rs<sub>1</sub>, and R<sub>5</sub> (Morgan and Comstock) of the may-flies corresponds to our Rs<sub>3</sub>.

a special group by Handlirsch, Protphemeroidea, which combines the characteristic venational features of the more primitive *Dictyoneuridæ* and the specialized features of may-flies, nevertheless they still are Ephemeroidea, which preserved only the anterior branch of M of the *Dictyoneuridæ* (MA). As to the dragon-flies, Needham's interpretation aroused doubts only in its application to the Zygoptera. The trachea which supplies RS in the latter arises from  $M_2$ , not from R, and in general no tracheæ which lead from R enter into the region of M. But Comstock and Needham think that here also, the vein RS enters into the region between  $M_2$  and  $M_3$ , and that trachea RS used to arise from R and cross the media, but later "detached" itself from R and "attached" itself to  $M_2$ . Since it is difficult to support the last supposition by definite proofs—there are none—Tillyard (15) and Rice (12) naturally expressed<sup>3</sup> doubts about the Zygoptera having RS. Munz, however, pointed out (9) that the conformity of the vein veins of Zygoptera and Anisoptera is so evident that it is impossible to interpret the venation of Zygoptera different from that of the Anisoptera, and accepted the old scheme of Needham.

As I approached the study of the venation of dragon-flies and may-flies I thought that if the dragon-flies and Ephemeroidea were Palæoptera,<sup>4</sup> *i. e.*, insects which never fold their wings on the back (roof-like) at rest, then not only the may-flies but also the dragon-flies should preserve the features of venation of the related Palæodictyoptera. If the venation of dragon-flies, according to the interpretation of Comstock and Needham, proves to be so unusual that it puts them in an entirely isolated group among the insects, the cause of such a situation evidently lies in the wrong interpretation of the venation by these authors and the uncertainties of the ontogenetic method. It is necessary to note that at one time Redtenbach (11) offered an entirely different interpretation of the venation of dragon-flies; attaching great importance to the alternation of con-

<sup>3</sup> Citing after Munz (9).

<sup>4</sup> Concerning the division of the Pterygota into Paleoptera and Neoptera, see my paper (7).

cavities and convexities of the wing, the author compared their dispositions in dragon-flies and may-flies, and came to the conclusion that they are very similar in venation as well as in the alternation of concavities and convexities. Unfortunately this author, following the erroneous conception of Adolf (1) concerning the different origins of "convex" and "concave" veins in the first stage of the "fan" type of wing and the disappearance in other insects of a series of "concave" veins, came to an incorrect homologization of the veins of the two groups mentioned with those of other insects. Thus the cubitus of Ephemeroidea (and dragon-flies) he indicates by the number viii, which in other insects corresponds to  $A_1$ ; the median by number vii, which corresponds to the cubitus, etc. Denouncing the earlier views of Adolf, Comstock and Needham also did not attach any importance to the similarity in the wing venation between the may-flies and dragon-flies, which was observed by Redtenbach.

It always seemed to me very risky to depend upon Comstock's and Needham's ontogenetic method for the explanation of the homology and evolution of venation. When we study the tracheation of nymphs and pupæ we study at the same time the ontogeny of tracheation, but not venation at all, because veins are vessel-like forms in which the blood circulates and into which nerves and usually tracheæ often enter; but there can exist veins without tracheæ. On the other hand, the thinner tracheæ which we observe in the nymphs and young imagines of dragon-flies and nymphs of may-flies go through the wing and outside of veins in great numbers and often do not connect the neighboring veins, but the ones lying far apart. As to the formation of veins, although it was previously supposed that they were formed originally by the tracheæ, more recent investigations have shown, especially in rather primitive groups [see, for example, the work of Marshall (17) on the development of the wings of the Trichoptera], that in the wing *anlage* the venation is formed before the tracheæ pierce through. Comstock and Needham supposed that the tracheation in the wing of a pupa and nymph reflects the primitive state of venation. Therefore one would suppose that in the forms with a venation which resembles

especially closely the scheme of the original venation, we should expect a particularly complete parallelism of the tracheation with the venation. But this is not so. In *Hydropsyche*, which is a small caddis-fly with extremely primitive venation, Comstock and Needham found a complete unconformity of the tracheation with the venation, which they interpret without regard for the direction of the trachea. These authors are obliged to do the same with the Hymenoptera and Diptera. Why should we rely so blindly upon the tracheation in case of dragon-flies and Ephemeroidea and ignore the data of paleontology, which proves the close relation of venation in contemporary representatives of dragon-flies and may-flies with that of the Palæodictyoptera (in the case of the Ephemeroidea, through the Carboniferous *Triplosoba* Handl.)? Such a "conception" is all the more unacceptable because the theory of Comstock and Needham encounters serious contradictions within the groups themselves. The crossing of the media which arises from R by means of the trachea RS takes place only in the Anisoptera; this does not appear in the Zygoptera, and the trachea of the corresponding vein arises from the branch M. We have no proofs that the latter condition developed from the former. As to the Anisozygoptera, in view of their very close relationship to the Agrionidæ (through the Lestinæ), one can suppose that in them the trachea RS of the authors arises from the media of the authors. A very diverse and changeable tracheation of nymphs of may-flies gives us still less right to conclude that they have such a crossing, that their complicated vein below R is M, etc.

My investigation of the relation of the venation to the tracheation has led me to the conclusion that the formation of venation occurred under the influence of causes of mechanical character; the tracheation, adapting itself to the newly formed distribution of veins, often changed in a most original way; therefore, one can judge the venation by such an "indirect" representation of it only with utmost care.

In view of these facts I decided that in investigating the venation of dragon-flies and may-flies, as well as of other groups, to turn first to the comparative study of the vena-

tion itself, at the same time constantly keeping in mind as much as possible the function of the venation, and changes which should appear in the phylogeny of the wing by the work of the separate parts of the wing and the work of its veins. Only after such investigation is it possible to approach the study of the history of tracheation, which depends upon the venation and reflects its history. This I will discuss at the end of this paper.

Let us first turn to the Palæodictyoptera. The "family" Dictyoneuridæ has the most primitive venation (figs. 1 and 2); the wings here are homonomous, hardly broadened at the base; sometimes their ends are somewhat pulled out and as if curved backwards (*Stenodictya*, *Microdictya*, *Stilbocrocis*, *Polioptenus*, et al). RS in the more primitive forms (*Stenodictya*, *Microdictya*) arises from R approximately at the middle of the wing, or a little nearer to the base; but in the majority of other forms we encounter the process of its receding towards the base. Usually RS sends 3 or 4 branches posteriorly, not counting its continuation; in some cases the second branch (counting from the base) does not reach the trunk RS, but adjoins to the first and sometimes (*Microdictya vaillanti*, *Stilbocrocis*, *Eumecoptera*) forks dichotomously. The media is divided into two branches, which we shall call M. anterior (MA) and M. posterior (MP)<sup>5</sup>; MA in this family, as well as in the majority of other Palæodictyoptera remains simple; MP branches in the Dictyoneuridæ, often forming three branches (*Stilbocrocis*, *Eumecoptera*, *Dictyoneurula*, *Acanthodictyon*, partly *Polioptenus*), in which it greatly reminds us of M in the Ephemeroidea. Normally the cubitus also divides not far from the base into two branches of which the first (anterior), CuA, usually remains simple as in *Polioptenus* and *Eumecoptera* (figs. 1 and 2); the posterior branch, CuP\*, usually gives rise to smaller branches.

In the very primitive forms the anal veins form a comparatively homogeneous series of 3-4 veins, which gradu-

<sup>5</sup> The development and configuration of the media have just the same characteristics as R. MA corresponds to the radius proper (R); MP, to the radial sector. The same was originally true of the cubitus (Cu).

\* Misprinted MP in original.

ally grow smaller nearer to the base; but the more specialized  $A_1$  is better developed, and others lose their independence, uniting either with  $A_2$  or even together with  $A_1$ .

There is no need to discuss the other families, because their wings were already specialized in different directions from those in which the dragon-flies and Ephemerids are specialized.

All recent Agnatha differ sharply from the Palæodictyoptera, in that their fore wings are greatly enlarged at the expense of the hind pair (fig. 4), which have become completely reduced in many species (in sub-group Bætoidea Ulm.). If the hind wings are present, the fore wings are wide and approximate a triangle; then, where the hind wings tend to disappear, the fore wings take the shape in the first group (Ephemeroidea and Heptagenioidea), which corresponds more to the shape of the fore and hind wings taken together.

If the hind wings of contemporary Ephemerids differ greatly from the fore wings, this was not the case in the past. In the Ephemerids of the Permian the hind wings differed very little or not at all from the fore pair, and their form resembled very much that of the wings of Dictyoneuridæ (13). Likewise, the wings of the remarkable Carboniferous Ephemerid *Triplosoba* Brogn. were homonomous (fig. 3). Handlirsch placed (6) this form into a special order, *Protphemeroidea*, because it preserved in its venation the features of the Palæodictyoptera, particularly of the Dictyoneuridæ. Just as in Eumecoptera (fig. 2) and in many other Dictyoneuridæ, RS arises nearer to the base and sends posteriorly the usual four branches, of which (and this is very important) the second branch, i. e.  $RS_4$ , originates near  $RS_5$ , and  $RS_3$  and  $RS_2$ , together with  $RS^1$ , form the distal group. Evidently  $RS_2$ , already forming the "inserted sector," did not reach  $RS_1$ . M, as in the Dictyoneuridæ, is divided near the base into the same two branches, MA and MP; MA also, as in the Dictyoneuridæ, remains simple, while MP is divided distally into three branches, the middle one and the two supplementary ones beside it being already changed into "inserted sectors" (Schaltsectoren). The close similarity of this MP with M in the real Ephemerids leads us to believe that M of

the may-flies is really MP, and their MA is reduced and has completely vanished. Cu is divided into two simple branches, in which one can also see CuA and CuP of the Palæodictyoptera. Then come the anal veins; the long  $A_1$  with its branches, and another long one,  $A_2$  or  $A_3$ , with its branches. The character of the cross-veins is the same as in Ephemeroidea. As already mentioned the fore and hind wings in the may-flies of the Permian were alike, their shapes quite resembling those of the Dictyoneurid wings; but in all that is known to us, MA was already missing. The branching of RS is also very much like that of Triplosoba and of the contemporary Ephemeroidea, while here also (*Protecha* Sell., *Prottereisma* Sell.)  $RS_4$  arises near  $RS_5$ , and the rest of the branches form the distal group. The branches  $RS_4$  and  $RS_2$  represent "inserted sectors" as in the recent Ephemeroidea.

According to the interpretation of Sellards and Handlirsch, Cu is divided into two branches at the very base; the anterior of these also divides into two side branchlets and a middle "inserted" one (in *Protechma*); and the posterior branch gives rise to two small branches directed posteriorly. The anal region is badly preserved. On account of this poorly preserved anal region it is difficult to say how to regard the two branches of the cubitus, whether they correspond to CuA and CuP of the Palæodictyoptera or whether there is another interpretation possible. Incidentally, the anterior branch with its branchlets is very much like the cubitus of Siphuridæ, Ecdyuridæ or Leptophlebiidæ.

The fore wings of the recent may-flies, because of the division of labor between the wings (all work of production of strokes and stroking the air being transferred to the fore wings), increased their dimensions and took the shape of elongate triangles, as in many Papilionidæ; as to the hind wings, where they are developed best of all—in Ephemeroidea and Heptagenioidea—they are of an oval or round shape as in many Rhopalocera, and in other may-flies—in Bætidæ, Ephemeroidea, and Cænidæ—they are subject to greatest reduction. The fore wings, substituting in these groups for the disappearing hind ones, grow wider in the cubital and anal region and take a shape which

corresponds to the form of the fore plus hind wings in other groups, or to one wing of the homonomous group (Dictyoneuridæ, Carboniferous and Permian Ephemérids). Therefore, I think that the primitiveness of Bætoidea wings is only an apparent one and that in the past their fore wings were also probably of triangular shape. The differences in dimensions and in the shape of both pairs, in their turn also, were formed for a second time, replacing the original homonomous condition. The venation inherited from the ancestors was not effected by the change in the shape of the wings, and it remained very much like that of such may-flies of the Permian as *Protereisma*, *Protechma*, and also as *Triplosoba*. The homologizing of veins in these last forms with those in the Dictyoneuridæ is therefore not difficult and is correctly interpreted by Handlirsch. RS in *Triplosoba* also turned off (from R) at the very base, but here the place of origin (how, is another question) is still nearer to the base. But more often Rs is derived (secondarily) from the basal part of M.\* The branching of RS is entirely similar to that of the Palæozoic may-flies and to that of the majority of Dictyoneuridæ, i. e., RS forms two groups: a basal branch, and another one almost always without a basal connection, the "inserted sector,"  $RS_4$ ; and the distal one, including  $RS_3$ ,  $RS_2$ , and  $RS_1$ , the sector  $RS_2$  having already lost its true origin ("Schaltsector"). In the hind wings, because of their reduction, the branches of RS are very seldom preserved, as in *Palingenia*; usually only  $RS_5$  and  $RS_4$ , and naturally  $RS_1$ , are preserved, but  $RS_3$  and  $RS_2$  retreat towards the edge and are reduced. M corresponds to MP in the Triplosobidæ and Dictyoneuridæ, and forms the usual three branches. The branches of M in the hind wings are reduced also, and usually are simple (fig. 10). At the base of the fore wings, M approaches R almost to contact, and weakening, disappears; in the hind wings M often fuses at the base with R. Into this narrow path RS is directed and usually diverges from M, but often ends here as an "inserted sector," i. e., it weakens and disappears, being joined basally with R and M by means of the usual cross-veins. In the hind wings,

\* Misprinted  $M_1$  in original.

RS arises either from R or oftener from M. As well known, RS and M are tracheated in the may-flies in the majority of cases from one main trunk, which turns away from the side trachea (in the body), independently from R. This condition and perhaps also the fact that RS oftener "turns away" from M, gave Anne Morgan the motive to assert that the complicated vein which Comstock originally (4) indicated as RS, is actually M. We shall return below to the explanation of this moving off of RS from M, but now let us turn to the following veins.

Cu arises near M and soon divides into two main branches;  $Cu_1$  and  $Cu_2$ , with an inserted middle branch which joins at the base either to  $Cu_1$  or  $Cu_2$  ("inserted sector"). In all Ephemeroidea (Palingeniidæ, Ephemeridæ, Polymitarciidæ, Potamantidæ),  $Cu_2$  forms a downward curve similar to the curve of the cubitus in dragon-flies. By means of its projecting angle, this curve approaches and often completely fuses with  $A_1$ . The cross-veins disappear between the very origins of  $Cu_1$  and  $Cu_2$ ; on account of this, in my mind, they correspond morphologically as well as physiologically to the triangle of the dragon-flies (Anisoptera). In Heptagenoidea and Bætoidea this curve is absent (except in Bætisca, Oniscigaster), or it is expressed very faintly. The basal bifurcation and the general configuration of the origin of the cubitus in Ephemeroidea are certainly secondary if compared to, e. g., their condition in Dictyoneuridæ. The condition in Siphuridæ (and perhaps in the Ephemerids of the Permian) is therefore less changed.<sup>6</sup> The peculiar condition in Ephemeroidea originated in the receding of the furcation point towards the base (this is a very common condition among the Palæodictyoptera, and in Ephemerids it unquestionably took place in RS), and by forming the curve in  $Cu_2$ . This connection with  $A_1$ , just as that in the dragon-flies, has unquestionably mechanical advantages, although the method itself and the original causes of the curve in  $Cu_2$  are not clear to us. It is difficult to say yet if one can see in our  $Cu_1$  and

<sup>6</sup> However, it is possible that in some Siphonuridæ the curve of  $Cu_2$  was lost secondarily; the condition in Oniscigaster is especially suggestive of this.

$Cu_2$  of the Ephemeroidea  $CuA$  and  $CuP$ . The similarity with the dragon-flies seems to confirm it, but their palæontological data do not assert this with certainty, and I indicate these branches so far by different symbols.

In groups with the curve of  $Cu_2$  present  $A_1$  also has a more or less considerable curvature. Often the descending segment of  $Cu$  fuses entirely with the original of  $A_1$ , a condition which we encounter in some Palingeniidæ (*Anagenesia*, *Plethogenesis*), or otherwise disappears (*Campsurus*, *Polymitarceus*, et al). Ordinarily  $A_1$  forms distally a series of branches directed posteriorly. It usually also has an upward curvature.  $A_2$  arises either in the middle of  $A_1$  and  $A_3$ , or very close to  $A_1$ ; usually it curves backwards soon after, and becomes short, and only in *Bætiscidæ* does it run parallel to the straight  $A_1$ .  $A_3$  is still shorter, but often has more branches; in *Bætisca* its first branch is parallel to  $A_2$ . From the distal part of these ( $A_3$ ) lead a few weak anal veins, but more often the latter lose their independence, and come in contact with  $A_3$  in different ways.

In groups which have the tendency to a final reduction of the hind wings, the cubito-anal regions of the fore wings grow, take the place of the disappearing hind wings in function, and correspondingly elongate and distribute the anal branches in accordance with the mechanical needs (*Cænidæ*, *Bætidæ*, *Leptophlebiidæ*). The anal veins preserve the more original bow-shaped form in the hind wings, but quickly weaken towards the base.

Now let us turn to the question of concave and convex veins, and to their relation to the veins in the wings of may-flies. In 1880 Adolf noted the fact that in the wings of may-flies the concave ones, like valleys, alternate with the convex, as longitudinal ridges. In the bottom of valleys and on the peaks of ridges are the adjoining longitudinal veins. Adolf regarded this alternation as very important. According to his understanding the "convex" and the "concave" veins have entirely different origins, significance and destinations. He thought that the original wings differed in the possession of a more regular alternation of the numerous convex and concave veins and that the wings

were similar to a fan. Redtenbach compared fully the distribution of these veins in the may-flies and dragon-flies, and found a complete correspondence. Later it was shown (2) that the indicated representation of Adolf was incorrect and perhaps this was the cause of Comstock's and Needham's paying little attention to the valuable comparisons of Redtenbach. The plaiting and alternative distribution of veins along the bottoms and tops has great mechanical value. The wings of the may-fly have attained a very high specialization. The membrane is extremely thin and delicate, and its veins have already adopted an extraordinary mechanical function and acquired the corresponding structure (ribs, absence of blood, dry structure) and their distribution also corresponds to the mechanical requirements. If this thin membrane were spread over the veins entirely in one plane, then at the stroke of the wings upon the air, being so delicate and unable to stretch, it would break and inevitably tear. The plaiting gives the membrane flexible, elastic qualities. At the sharp resistance of air on the stroke of the wings, the latter can stretch sufficiently because of the plaiting at all necessary points. In the formation of this plaiting the closely lying veins, as in similar cases (Arthropoda), were distributed, some on the bottom, others on top, and their course, even in their details, was affected by the plaiting; the fundamental character of the latter, in its turn, was conditioned by the original distribution of veins. In that way the continual reciprocal action of these two structures took place in the course of evolution. The concave position among the main veins includes Sc, RS, Cu and  $A_2$ , and then a series of distal branches, which alternate with the convex greater part of the distal sectors,  $Cuad^7$ , Mad,  $RS_4$ , the  $RS_3$  concave,  $RS_2$  convex; among the smaller distal sectors, the larger ones also alternate. In the more primitive Palpingeriidæ, Ephemeridæ, Ecdyuridæ and the ones near to them, which retain rich, thick venation in their wing, the greater part of the distal sectors,  $Cuad^7$ , Mad,  $RS_4$ , the branches between  $RS_2$  and  $RS_3$  as well as these branches

<sup>7</sup> Cu additional or M additional; in this way we shall designate the middle branches of Cu and M.

themselves weaken at their origin and appear to be tied to the neighboring veins only through common cross-veins; and already have no real basal part of their own, nor any origin. Such absence of the origin is unquestionably a secondary condition. In *Palingenia* and in some *Ephemera*,  $RS_4$  arises normally from the trunk  $RS$ , but in others its origin disappears. The same seems to be the case with other sectors. In the specialized *Bætoidea* this process went still further, and in *Bætidae* all the longitudinal veins except the main ones ( $Sc$ ,  $R$ , \*  $RS$ , \*  $RS_5$ ,  $M_1$ ,  $Cu_1$ ,  $A_1$ ,  $A_2$ ,  $A_3$ ), lost their origins and became "independents," Woodworth (16) and the distal ones became shorter and shorter and deteriorated into a series of small veins along the edge, like the measurements on a ruler. How can one explain such a change? It can be satisfactorily explained through mechanical and practical means. The longitudinal veins lose their origins where they enter by means of their bases into the space between the branches of the forking vein, which forms a sharp angle, for example,  $RS$  or  $M$ . Such a vein is of course always "convex" if the dictomating one is concave, and vice versa. Because the part of support rests always upon the branching vein, the mechanical meaning of the basal part of the intervening vein diminishes and becomes insignificant; consequently the basal part of such a vein weakens, becomes thinner and disappears entirely. The economy of material requires the disappearance of the unnecessary part of the vein. Everyone knows that in the more specialized and (so to speak) "mechanized" wings, as those of the *Bætidae*, all superfluous veins disappear, and the remaining ones tend to keep the intervals between themselves equal. If the origins of the "inserted sectors" remained, this would be an injurious accumulation of veins in different places. The disappearance of the base also requires the alternative distribution of veins in different planes. If the vein is "concave," and the "inserted" vein, e. g.,  $RS_4$ , is "convex," then near the union with  $RS$  the short and weak part of the base would have a broken-up aspect (from the convex side to the concave). The mechanical meaning of this broken-up part is insignificant, therefore it

\* Misprinted  $R_1$ ,  $RSc$  in original.

would unquestionably weaken and finally disappear. Such was, according to my understanding, the way in which the "inserted sectors" of the German authors were formed.<sup>8</sup> Now, the origin of RS sometimes from M, more seldom from R, or its "free" origin becomes clear to us. Entering into the oblique angle between the convex R and M, the concave RS unquestionably had to become a "Schaltsector," which we quite often find in the typical species of *Hexagenia*, in some *Siphylurus* and others. The approach of the base of RS to one of the neighboring veins, e. g., to M, together with some small changes in the direction of the joining cross-vein (the cross-veins are certainly preserved) easily give the appearance that RS arose from M.

The appearance of the alternation of the convex and concave vein with its result—the change of convex veins into "inserted sectors"<sup>9</sup>—had been acquired by the ancestors of may-flies and dragon-flies very long ago. This appearance was well expressed not only in the may-flies of the Permian, but also in the Carboniferous *Triplosobidæ*, as becomes clear from their possession of a series of "inserted sectors." The dragon-flies of the Mesozoic do not differ in this respect from the recent ones. The Carboniferous "Protodonata," at least some of them, also acquired this alternation. The plaiting was already indicated in the Palæodictyoptera and Megasecoptera but it was very seldom that the branches actually turned into inserted sectors, and according to the branches we can judge with certainty about this

<sup>8</sup> Woodworth, on the contrary, sees in the "independent" veins of the may-flies primitive structures which illustrate the process of the formation of the longitudinal veins of insects. The "independent" veins are supposed to receive their origins from the marginal vein, as growths of the latter to the inside; these growths are pulled out towards the base and finally fuse with one of the main trunks. The media, according to Woodworth, was formed as an independent vein also, only the anal veins having a different origin, and growing from the base. We have no need to stop to discuss this fantastic theory; it contradicts all data of paleontology and comparative systematics (the condition in *Bætoidea* is unquestionably secondary!), and is impossible from a morphological aspect. (One cannot imagine the growth of veins in the membrane.)

<sup>9</sup> I do not exclude the possibility that some (short) intercalary veins of dragon-flies could develop as illustrated by Comstock (1918): as a result of the formation of plaiting.

plaiting. Such was the situation acquired, e. g., in *Camplyoptera eatoni* Brongn., a species referred by Handlirsch to the Megasecoptera. In the drawing by Handlirsch the character of the intercalary sectors is very clear. Furthermore, according to Handlirsch's drawing the change of some longitudinal veins into intercalary sectors had begun in *Lycocercus* and in *Epithete*. In other Palæodictyoptera we do not notice this. In groups rich with longitudinal veins as the Spilapteridæ, Lamproptilidæ, Polycyregridæ, the plaiting was already suggested, but it never came to a formation of inserted sectors. The plaiting, together with the forming of inserted branches, is a very important mechanical improvement, which allowed lightening of the wing a great deal without loss of its firmness and elasticity.

Leaving aside for awhile the question of the origin of the peculiarities of tracheation in may-flies, which we will consider together with the tracheation of dragon-flies, let us turn to the venation of dragon-flies. The peculiarities of dragon-flies enumerated at the very beginning of this article, are, as stated, rather the peculiarities of interpretation, which result from the nature and insufficiency of the method employed ("method of ontogeny"), and not at all from the actual venation. Putting aside these hypothetical considerations, let us compare the wings of dragon-flies with those of may-flies and Palæodictyoptera.

First of all one should note that in form as well as in the general distribution of the main longitudinal veins and in the smaller reduction of the anal area, the Anisoptera show a great deal more primitive features than the Zygoptera, whose wings were subject to very great changes; one could say that in the Anisozygoptera everything in general is much closer to the Zygoptera, and as a matter of fact merges into them in their more primitive Liassic representatives (Archithemidæ, Heterophlebiidæ); they still partly resemble the Anisoptera in their form, configuration of the anal area, and in general distribution of the main veins.

In this collective Liassic complex the triangle (e. g., in Heterophlebiidæ) begins to take form, but further development was reserved only for such groups in which the triangle succeeded in acquiring its typical aspect,—and these were the groups that formed the Anisoptera; others, where

the "attempts" did not lead to the form of a typical triangle, died out. From here by way of another evolutionary path of the Zygoptera, were derived the majority of the known Anisozygoptera, which often cannot be told apart from the Zygoptera.

Unquestionable Zygoptera and Anisoptera are known only as far back as the Jurassic. The form of the wings in the Anisoptera and still more in the primitive Archithemidæ, resembles very much that of the wings of the Dictyoneuridæ, the most primitive of the Palæodictyoptera, also the Spilapteridæ, Triplosobidæ and may-flies of the Permian. If these dragon-flies have remained unchanged in their original form and homonomous nature of wings, we have also the right to expect a general plan of the distribution of veins, because the one and the other are bound together by function. This we actually find takes place. In Diastomma (Archithemidæ) no nodus is to be found and Sc has the same aspect and same relation to R as it has in the majority of Dictyoneuridæ and Spilapteridæ. The next longitudinal vein after R gives rise to 3 or 4 branches; their method of origin and general distribution repeats that in a series of Dictyoneuridæ and Spilapteridæ (e. g., in Stenodictya, Polioptenus, Acanthodictyon, Eumecoptera and others), and still more of Triplosoba and the Agnatha. The resemblance of the Triplosobidæ in the distribution of the branches of RS, especially to the Anisoptera, and to the recent may-flies is so striking and obvious, that we can compare vein by vein without difficulty. In the dragon-flies we usually find in the region of RS two groups, the basal,—formed by the *first* concave branch, as in may-flies ( $RS_5 = M_3$  of authors); and the *second* convex and also usually "inserted" branch ( $RS_4 = 1$  Morgan); and the distal group, formed by the concave  $RS_3$  the weak convex and sometimes almost disappearing inserted  $RS_2$ , and lastly the concave continuation of RS (as in may-flies and Triplosoba). After this complicated RS follows the simple vein which is divided from it at the very arculus, and which is indicated by Odonatologists as  $M_4$ , but which represents M. It is still impossible to say whether this M corresponds to MA or MP of Triplosoba, and that is why we shall indicate it simply by the letter M. At its base M turns sharply towards R

(as in may-flies) and almost fuses with it, but not entirely: by looking from above (partly), and in a cross-section the partition between the two veins is still distinct. The origin of RS from this turning-point of M, which sometimes has the form of a cross-vein, is not clear to us. RS arises here from the base of M just as in may-flies and one certainly should look upon such a manner of origin as a secondary appearance, even if this tendency was acquired very long ago, for it was already present in the dragon-flies of the Liassic and Jurassic. After this vein follows Cu (CuP) which forms in the Anisoptera and Anisozygoptera, soon after its origin, a more or less sharp curve or projection posteriorly, as in the suborder Ephemeroidea. This curve is still entirely distinct in the Agrionidæ, which appear to be the continuation of the Anisozygoptera, and disappears only in the species of Calopterygidæ (by the "straightening" of Cu and A).

Now, if we compare the relation of the longitudinal veins to the convexities and concavities in dragon-flies to that in may-flies, we will ascertain the identity of their distribution, which was well explained by Redtenbacher. This circumstance, certainly, proves once more the correctness of our comparison of RS in dragon-flies (=M of the authors) to RS in may-flies, etc. Cu (Cu+Cu<sub>1</sub> of the authors) is concave, as in the may-flies, and the next vein after it, which consists of the "anal bridge"+Cu<sub>2</sub> of the authors, forms the same kind of projection and is just as "convex" as in Ephemeroidea Ulm. This vein is unquestionably A<sub>1</sub>, and Cu<sub>1</sub> of the authors is Cu<sub>2</sub>, and to be even more exact, it is CuP. In the majority of the Anisoptera, A<sub>1</sub> comes into contact with Cu after the projection, but such contact, which often changes into fusion, is also frequent in the Ephemeroidea. On the other hand, in the majority of Zygoptera and Anisozygoptera and many other Anisoptera (compare Fig. 6, wing of fossil *Heterophlebia dislocata*, with Fig. 7, hind wing of *Phyllopetalia apicalis* Seyls), A<sub>1</sub> does not come in contact with Cu and runs independently and almost parallel to Cu. In its general appearance of A<sub>1</sub> (Cu<sub>2</sub> of the authors) of the dragon-flies, especially such as the Gomphidæ or Anisozygoptera, corresponds entirely to A<sub>1</sub> of may-flies, analogously forming an arch towards the front and analogously sending a

certain number of weak branches posteriorly. Next follows in the may-flies the concave  $A_2$ , then the convex  $A_3$ . But even if these veins did exist for a long time in the dragon-flies, they are fused now with  $A_1$  at the base, and in the majority of cases this region has suffered great reduction. Usually we still find in the hind wings of the Libellulidæ two longitudinal veins, still quite distinct, which arise from  $A_1$ . As we find the suggestion of a fusion of the two longitudinal veins with  $A_1$  in the "Protodonata" also, the conception of the composite nature of A becomes possible.

We did not finish the investigation of Cu and the triangle. The triangle represents a frame which presses apart and at the same time strengthens Cu and M. The perfection of this frame in the Anisoptera evidently becomes an acquisition of importance and use in the mechanism of the wing. We find the formation of the triangle in the Archithemidæ and Heterophlebiidæ in *statu nascendi*. Its forms here were rather diverse, sometimes different in the fore and hind wings, and in general these triangles did not correspond entirely to the triangles of the Anisoptera. These groups with the aberrant triangle died out, and only the groups with the normal triangle were developed and became preserved up to the present time. In the series of Anisozoptera-Zygoptera no triangle was formed, but in connection with this the original form of the wing is also not preserved, the venation, changed greatly in the anal area, became reduced, Sc became shorter, etc. But originally, as we notice in the Lestinæ and in the related Anisozygoptera, the distinct projection of Cu (and  $A_1$ ) was here also. The same kind of projection is also clearly expressed in the very conservative group Ephemeroidea Ulm. The triangular area between the bases of  $Cu_2$  and  $Cu_1$  in the families of this suborder also closely resemble the triangle in the dragon-flies, only its external side in the former is represented not only by one straight vein, but by two cross-veins (between  $Cu_1$  and Cuad,  $Cu_2$  and Cuad), which are seldom placed opposite each other. The "inserted sector" Cuad is also often found in the Anisoptera; it is also well repre-

sented in the fossil Heterophlebiidæ<sup>10</sup> by a longitudinal and usually uneven vein anterior of Cu. All these comparisons lead to the conclusion that in the dragon-flies, Cu<sub>1</sub> of the authors is not at all Cu<sub>1</sub>, but that it corresponds to Cu<sub>2</sub> of the may-flies. Cu<sub>1</sub> of the may-flies does not exist any longer in the dragon-flies.\* It is very possible that Cu<sub>1</sub> of the may-flies is CuA<sub>1</sub>, but at present we cannot ascertain this.

The top side of the triangle was formed, according to Needham, by a cross-vein between Cu and M, slanting distally<sup>11</sup>. This is contrary to certain facts. In *Neurothemis oculata* Fab., for instance, and even more in *Aeschnidium*, the region of the triangle, as well as other areas, is occupied by a thick net and between M from one side, and Cu and the top side of the triangle from the other side, is distributed a thick series of short cross-veins. It is absurd to attribute the formation of the upper side by an inclination of a cross-vein. The outside as well as the upper side very likely was crystalized, as it were, directly from the network (certainly of very fundamental origin) under pressure of mechanical causes. Furthermore, this vein exists in order to join the basal part of Cu with M. If it came into that position by the slanting of a cross-vein (between Cu and M) one would not understand how it could pass by M and terminate on the exterior side of the triangle, a short distance down from M; this condition one encounters sometimes in the Libellulidæ and we find it in Heterophlebia, where it goes to the exterior side and is almost parallel to M (hind wing, *H. dislocata*). Such diversity points to the diverse nature of the formation of this vein. As soon as this wing-structure, which was derived from the configuration of the venation and of the wing form and for the working of its parts, acquired the formation of a triangular frame, its two sides (the interior side is formed by the downward projec-

<sup>10</sup> E. g., *Heterophlebia dislocata* (Handlirsch, l. cit., pl. 42, fig. 3).

<sup>11</sup> Needham, l. cit., p. 717, fig. 12.

\* At the request of Dr. Martynov, the following sentences, which were in the original, have been omitted: "In the Protodonata (Meganura, Boltonites, Typidæ) we also usually find the simple anterior branch CuA<sub>1</sub>, and the branch CuP joined to the anal group. This seems to point to the conclusion that Cu<sub>2</sub> of the dragon-flies is CuP, and that CuA disappears in them."

tion of Cu) begin to form themselves from the veins existing there, no matter which ones. It seems to be not an impossible idea that the upper side in some groups could be the remains of the original part of Cu<sub>1</sub>. Cu<sub>1</sub>, as in the may-flies, had to be concave, and this top side is concave, changing at the end into a sharply convex M. The fact that its end does not reach M would therefore be comprehensible. On this theory I do not insist because I cannot offer any definite facts of proof.

In the Zygoptera the true triangle does not exist, but in the Agrionidæ—and they form the main part of the Zygoptera—a structure was formed which in its function, to a certain degree, replaces the triangle. This is the “quadrilateral,” which hereafter takes the form of a narrow triangle. It is very certain that such a structure as it is represented in the Lestinæ, for instance, does exist, and is indicated by the fact that from the Anisozygoptera up to the present time only such a form as (*Epiophlebia suprestes* Selys) was preserved, where the “quadrilateral” has a form identical with that in the Lestinæ. Where the projection of Cu was not fixed by the formation at this place of the frame of a triangle, or quadrilateral of the type of Lestinæ, there the existence of this projection, and below the projection of A<sub>1</sub>, lost its mechanical significance. More than that, this projection because of the functioning of this vein would be entirely without purpose and even harmful. It is not surprising, therefore, that in the Calopterygidæ, where the “quadrilateral” did not adopt the form as in the Lestinæ and *Epiophlebia*, Cu tended to straighten itself out in diverse ways; a tendency which reached its maximum development in Calopteryx and related forms.

Preceding the above discussion, I compared the venation of the dragon-flies with the venation of the Carboniferous Prophemeroidea (*Trilobosoba*) and through them to the Dictyoneuridæ. I referred little to the Protodonata because the evolution of their wings was along different lines from the dragon-flies. It is true that in part of them two branches of M are represented as well as the two branches of Cu, which do not exist in the Odonata; but in other respects they are more specialized and go further than the dragon-flies from such groups as the Dictyoneuridæ. One

can say that the primitive net of their wing was used for the formation of secondary longitudinal sectors, which imitate and take the position of the original ones. In contrast to what was as a rule expressed in the evolution of the Palæodictyoptera, may-flies, and dragon-flies, Rs did not expand, but decreased. In these the distribution of branches of RS and also  $M_1$  and Cu is more pronounced than in the Odonata, and departs from the distribution which we find in the Dictyoneuridæ and Protephemeroidea. In this respect the Odonata have preserved more of the primitive features. The one-sided and extreme specialization of the wing venation of the Protodonata, with the loss of some fundamental features of their ancestors, were probably one of the main causes which brought about the rapid extinction of the group.

From the base of the Odonata there separated off, probably some time before the adoption of the main features of the recent venation, one more group known to us through a single representative from the Liassic—*Protomyrmelon brunonis* Geinitz. The wing venation of this form was figured by Handlirsch on Pl. 42, Fig. 14, and is reproduced here in Fig. 8. Some superficial resemblances with the Zygoptera, and at the same time some singularities of venation, lead the author to isolate the species in a separate sub-order, Archizygoptera. Sc is very much shortened and Rs and M very strongly distorted, so it is difficult to understand their distribution. Handlirsch represented Cu as two-branched; below it came the anal. If Cu is actually composed of two branches, then this fact, together with the peculiar structure of RS and M, would be sufficient for us to place this form into a separate order by itself. But one should note that the base of the wing is not well preserved in the fossil.

Now let us look briefly at the tracheation of the wings of the may-flies and dragon-flies. Such an inquiry is natural. If our interpretation of the venation of the dragon-flies and may-flies is correct, how can we explain, then, the way the trachea of RS runs in the anisoptera, where the trachea which arises from R is opposite the nodus, crosses  $RS_1$  and  $RS_3$  and enters into the vein  $RS_4$ , extending, and often a great deal, from its base? How can we explain the almost regular

absence of the trachea in  $RS_1$  of may-flies, and also of a series of distal branches chiefly convex, as in Agnatha, Odonata, etc? Let us try briefly to throw some light on the question; and let us start with the may-flies.

A characteristic feature of the tracheation of the *anlage* of the nymphal wing<sup>12</sup> appears to be its exceptional diversity in different groups and its marked instability, which is shown in a very great individual variation. By studying the tracheation in different groups and comparing it with the venation, we observe in the diversity a definite correlation with the peculiarities of venation. I base this statement upon the work of Morgan, who gave a series of illustrations of the tracheæ of nymphs of different may-flies, as well as on my observations. Only in some of the more primitive forms and then only in the early stages of the development of the wing *anlage*, do we encounter, as shown by Morgan, in Chironetetes, for example, the normal full tracheation, with the penetration of the tracheæ into all longitudinal veins through their bases. In the later stages of development of the same Chironetetes the part of the trachea which goes into  $RS_1$  (=  $M_1$  Morgan) disappeared and instead of this a series of small tracheæ was directed into the vein  $RS_1$  from the neighboring, stronger trachea R. A quite full tracheation exists according to Morgan in Heptigenia sp. (P. 5, Fig. 3), but here the tracheation in  $RS_1$  and also in some other small branches has already disappeared. I repeat, we seldom encounter normal tracheation. In most of the may-flies we usually encounter a regular alternating of veins in which the tracheæ normally penetrate through the bases with veins which have no such tracheæ, and which are tracheated by numerous small branches from tracheæ of the neighboring veins (see e. g., Fig. 11, which illustrates the course of tracheation as in species of Heptigenia Ulmer). Almost always the vein (with a few known exceptions in Chironetetes and Heptigenia) which is tracheated

<sup>12</sup> If the tracheoles are distinguished with difficulty in the wings of the imagines of dragon-flies, then it is still more difficult in the may-flies. However, the characteristic features of the venation and tracheation of the adults are already indicated in the nymphs, and for that reason we shall investigate the imagines instead of the nymphs.

by such means and which was one of the first to lose its own trachea, is  $RS_4$  (=1 Morgan); that is the vein which has no normal tracheation in Odonata, where it receives the trachea either from  $RS_3$  (Zygoptera) or from R (Anisoptera). Furthermore, the convex vein between  $RS_4$  and  $RS_1$  is tracheated (almost exclusively) in the same way. Tracheæ which go into M and R are often very weak also, or even vanish entirely (especially in M), and in such a way these veins adopt a secondary tracheation from the branches of the neighboring trunks. The intercalary vein in  $Cu_1$  is similarly tracheated, sometimes  $A_1$  also. If we compare such characteristics of tracheation with the characteristics of venation, then without effort we shall notice the fact that the first veins to lose their own trachea and begin to be tracheated by small branches from neighboring trunks are all veins which were made "inserted" (independent, intercalary, Shaltsectors, etc.),—that is, which lost their origins. Such veins as far as known are almost always convex veins. Furthermore, in the more primitive species groups as Bætoidea, but also Siphoneuridæ and a few Ephemeridæ, the tracheæ which go into M and R, that is already into the main but exclusively convex veins, are weakened and eventually disappear. We have said above that because of this loss and even by the weakening, of trachea as in the case of R and M, which penetrate into the vein through the base, this vein begins to be tracheated by small branches from the neighboring tracheal lines. The tracheation of such "inserted" veins is, however, very diverse, because branches penetrate into it not only from neighboring systems but also from trunks which lie further away anteriorly and posteriorly. Such small branches must quite often go a long way around before they come into the necessary vein. Quite often some small tracheal branches, which are derived from the neighboring trunks as well as the trunks placed further away, become a great deal stronger than others, and accept the chief burden of tracheation; in such cases one or the other part, and sometimes most of the small tracheal branches, are subject to reduction. Finally, not rarely there are cases when only one trachea receives the repossession and tracheates almost entirely a given vein (a certain part of the

small branches or neighboring trunks nevertheless remain). The methods of tracheation, as it was noted above, are very diverse in general and subject in particular to a strong individual variation. The one or the other vein is tracheated sometimes only by small branches, sometimes also by larger ones. The latter penetrate either from the nearer or from the further lying trunks, etc. Evidently a series of causes not considered here (that is, certain circumstances), influence the distribution of smaller branches. Sometimes, however, the one or the other method of tracheation is understandable. In a number of forms, as noted, the trachea RS does not continue into the distal branch  $RS_1$ , but turns off into  $RS_3$ , and  $RS_1$  is tracheated by small branches. This we will understand if we remember that alongside RS there runs the trachea trunk R, which can supply  $RS_1$  with branches. However, when R disappears, the trachea  $RS_1$  is usually preserved. Morgan, seeking for an analogy with the dragon-flies, noted that in one species of *Heptigenia* and only in part of these specimens, the tracheæ which supply  $RS_3$  (=RS? Morgan) separate not only from the trunk RS, as usual, but also from R. Desiring to see in this the analogy with the Odonata, Morgan concluded that this vein is  $RS_3$ , and that here we have a preservation of the crossing of the tracheæ and veins, which sometimes took place in the may-flies and now in dragon-flies.<sup>13</sup> It is not necessary to say that such a conclusion, which is now supported by Comstock (3), has not enough foundation. In all may-flies the concave  $RS_3$  is tracheated in a normal way from a concave trunk RS (=M<sub>1</sub> Morgan and Comstock), as it should be, and only in part of the specimens of *Heptigenia* studied the strongest trachea appears to be a branch of R. Taking into consideration the unusually great amount of variation in general, and the capriciousness of the tracheæ, can one attach such great significance to this exception, and conclude that this condition once existed in all may-flies, i. e., that in all may-flies RS takes root in the region of the media? Evidently such a con-

<sup>13</sup> Only in the Anisoptera. Morgan says that the crossing was unquestionably present in the Zygoptera, but that is pure hypothesis which has no supporting facts and is more than doubtful.

clusion is very daring and was prompted by the wish to find a full analogy. However, Morgan is wrong in supposing that by such an interpretation a full analogy with the dragon-flies is established, because RS of the may-flies is a concave vein and corresponds completely to a concave vein in the dragon-flies, i. e., to  $RS_3$ ; but not to the convex vein,  $RS_4$ , which almost always has the character of a "Schaltsector," and which, according to the understanding of the authors is a branch of R,, i. e., RS. To this vein there entirely corresponds in the may-flies another convex vein, also always inserted, which Morgan indicated as I and Comstock as IRS (intercalary). If one attaches importance to such exceptional cases of the entering tracheal trunks, then we lose any support of the theory of the establishment of homology of the veins. According to the illustration of Morgan (Pl. 5, fig. 7) in *Epeorus humeralis*, the vein 1 is supported in the distal part by one trachea from  $M_2$ . Why in such a case should we not consider vein 1 (that is,  $RS_4$ ) to be only the branch of  $M_2$  (that is,  $RS_5$ ) and its basal part as a bridge? In *Blas-turus*, according to the same author (Pl. 6, fig. 27), the middle (interia) vein of the media is tracheated by one trachea which separates from  $RS_5$  (=  $M_2$  Morgan). Why not suppose that the crossing once existed here, and not consider that this vein is a branch of  $RS_5$ , etc.? Such a supposition is not more unlikely than the one assumed by Morgan.

I have already noted above the fundamental nature of the relationship between the tracheation and the character of the venation. *Those veins which have lost the normal method of origin from other veins and become "inserted sectors," that is, after weakening at the base, have lost the base itself, those veins have lost the normal mode of tracheation and acquired a secondary tracheation.* Such veins are the convex branches and also some small secondary, distal, concave branches. It is true that not everywhere the convex vein-branches changed into "inserted sectors"; there are exceptions, though very seldom. Thus in *Palingenia*,  $RS_4$  in the fore wings<sup>14</sup> originates nor-

<sup>14</sup> In the hind wing this vein is already a typical inserted sector.

mally and has not yet changed into a typically inserted sector. Nevertheless, here this vein takes a definite convex position and forms at its base a projection towards the concave vein R. This is sufficient for the secondary tracheation to be adopted. The main convex veins, R and M, had originally and have still in many species their own tracheal trunks, which penetrate into them; but in the other weaker tracheæ and in the more specialized groups, as in Bætoidea, for example, where the membrane is very fine, all superfluous veins are discarded and in the remaining ones the alternation of convexities and concavities is sharply expressed up to the very base, where the main convex veins, R and M, lose their own tracheæ.

The indicated relation becomes clear to us, if we look at it from an historical point of view. There was certainly once a time when the alternation of convex and concave veins was only suggested. There was still<sup>15</sup> no inserted sectors, and the present convex  $RS_4$  and  $RS_2$  of recent types had a normal origin from R. Because of the absence of plaiting of the wings and the diversity in the methods of origin of the different veins receiving the trachea normally (that is, through the base from larger trachea of other veins of which they were branches), this position of the tracheation is approximately preserved at the present time, as mentioned above, in a great many primitive forms, and also in the earliest stages of development of the wing *anlage* in nymphs. As the wings "mechanized" more and more, that is, as the membrane became finer, the veins adopted an alternation of convex and concave positions, the basal part of the veins at the time of the change from the concave position (e. g., of R to  $RS_4$ ) weakened and finally was obliterated. The normal tracheation through the base into the convex vein became more and more difficult, and then became impossible, when the vein

<sup>15</sup> By this I do not mean to say that all, even the smallest irregular distal veins, were originally normal branches which arose from other veins. Small branches were formed at their places from the primitive network, were unstable, irregular, diverse and as a rule gave rise to no (secondary) alternation of convexities and concavities. Now, as before, they are tracheated by small branches probably in very diverse ways. These supplementary, secondary veins I do not consider here.

lost its base. This condition was carried over into the nymph, where in general there was at once laid down the foundation of imaginal venation. Such convex veins had to acquire a small tracheal supply by some other means. The small tracheoles in may-flies and dragon-flies (in nymphs and young imagines) frequently separate from the longitudinal trunks, and by means of the cross-veins usually reach the neighboring trunks. When the basal tracheal trunks began to weaken the small side branches of the neighboring trunks began to strengthen in their place, and finally to replace them completely in function. Because of causes which we cannot consider further, one or the other branches strengthened to the disadvantage of the others; and sometimes the tracheation, chiefly in one trachea which arose either from a neighboring or a remote trunk, appeared to be the most preferable. Since the strengthening of some of the small tracheæ depends upon a thousand small causes, because of their multitude and original similarity, even in the development of one individual, it is natural that the secondary tracheation had to be a very diverse and variable one. Under such conditions in the interpretation of the venation one should not attach any importance to the fact that in a certain species a vein receives its secondary tracheæ from neighboring trunks and not from the side where it should be. Such appears to me the origin of the secondary tracheation of may-flies; and if this idea is correct for the may-flies, then it is also correct and entirely applicable to the dragon-flies.

In dragon-flies the whole character of the tracheation of the wing in its relation to the venation maintains in general the same character as in the may-flies, since the dragon-flies have much less diversity and much more stability in tracheation than the may-flies. The tracheation of R is preserved everywhere, which is comprehensible to a certain degree if we consider the shortening of the subcosta in the dragon-flies. The tracheation of M is also preserved, although in the Zygoptera it is sometimes greatly weakened. The convex  $RS_2$ ,  $RS_4$  and  $A_1$  obtain a secondary tracheation by small branches from the neighboring tracheæ; the cross-tracheæ are of course supplied by the small supplementary distal, longitudinal veins. The media

in the *Zygoptera* is supplied by its own trachea as well as, to a greater or less extent, by the small branches of the neighboring veins.  $RS_2$ , together with a series of other veins in the region of  $R_s$  and  $M$ , are supplied by small tracheoles (see fig. 9), but in *Zygoptera* the vein  $RS_4$  is tracheated in this way at its basal part, while in its distal part usually (but with exceptions) by one fairly large branch which arises from  $RS_3$  (fig. 9). In the *Anisoptera*, this same  $RS_4$  receives its trachea from  $R_1$ , and even the basal part of this vein (the "bridge") is tracheated chiefly by the branch of the tracheæ directed posteriorly. Comstock and Needham conclude from this fact that the vein  $RS_4$  is actually  $RS$ , which takes root in the region of the media; and they extend this conclusion to the *Zygoptera*, in which this type of tracheation of  $RS_4$  was never observed. From my historical point of view, such a tracheation of  $RS_4$ , and in particular the difference in both suborders, becomes generally clear. The convex branches of  $RS$  and also  $A_1$  for the same reasons as in may-flies lost their original and normal mode of receiving tracheæ and acquired a secondary tracheation at the expense of the ever-increasing small branches from the neighboring trunks, which used to enter here before. Such a method of tracheation was preserved in the basal part of  $RS_4$  in *Zygoptera*, but in the greater distal half one trachea which separated from  $RS_3$  became predominant. This acquisition of predominance by one or several branches in dragon-flies as well as in may-flies, is often found in the distal longitudinal veins, and there is nothing surprising that one of the tracheæ strengthens at the expense of the other in  $RS_4$ . Originally, when the present-day type of tracheation was only beginning to evolve, the greater diversity probably took place here, as in the may-flies. Having lost its tracheation,  $RS_4$  received at first the tracheoles from the neighboring trunks as well as from  $R$ , and in the same group some tracheal branches obtained predominance; and in other groups, other branches, etc. The tracheation of  $RS_4$  in the *Anisoptera* from  $R$  was at last established (why, is another question); in *Zygoptera*, partly from  $RS$  and partly by the mere preservation of an earlier means of supply by small tracheoles (in the basal half). It is difficult to say why the tracheation of

$RS_4$  by the branch from R or  $RS_3$  (almost) was established, but I think that the formation of a stable point of supply at the nodus had great influence upon the process of acquiring such a tracheation. In the Anisoptera the point of origin of the branch in  $RS_4$  from the trachea R is just opposite the nodus. In the region of the nodus the wing is certainly stronger, is much less able to bend, and is much less exposed to occasional deformation at its distal point. The trachea which arises from this place in R is naturally more protected at its base and therefore more able to be strengthened and preserved than other more distally lying branches from the neighboring trunks. In the Zygoptera  $RS_4$  is supplied by an entirely different trachea; this is from  $RS_3$ , but here also the place of origin of the trachea is opposite the nodus, though a little more distal. However, one should bear in mind that in the evolution of the Zygoptera, there took place migration of the nodus towards the base, so that the separation of the point of origin of  $RS_4$  and the nodus becomes clear. The difference between these suborders in the tracheation of  $RS_4$  proves my supposition about the original diversity and the probable variability of the growing secondary tracheation in the dragon-fly. It would be strange if in both suborders, which are so different on the basis of their venation, there should have been established a similarity of  $RS_4$ .

Unquestionably the tracheation is also secondary. This tracheation in general is similar in both suborders, but there are a few which are somewhat inconsistent. The tracheation of the wings of dragon-flies differs in general from that of the may-flies in its stability; but the stability is not so great as one would think and one encounters in the Anisoptera, a variation of even a serious character. I did not investigate these questions specifically; I shall mention only four young nymphs of *Æschna* sp., which were taken together in the fall of 1923 in a little pond near Lakhta; in one of these the tracheæ appeared to be anormalous in the following features: in the left fore wing the trachea R behind the nodus gives rise to a strong trunk, which at once separates again into three branches, entering into  $RS_4$ ,  $RS_3$  and  $RS_1$ . Only  $RS_5$  is tracheated here from the trachea of the media. In the right hind

wing the trachea which supplies our M ( $M_4$  of the authors), appears to be free up to the very base, and arises only very near the trachea RS (fig. 12). The last variation is especially interesting as indicating that the origin of the trachea M from the general trunk  $Rs_4M$  is perhaps the result of a secondary fusion of the base of the trachea M with the base of RS.

And so the investigation of the tracheation of the wings of dragon-flies and may-flies from a functional and historical point of view leads us to the conclusion that the peculiarities were developed in connection with the acquisition of the characteristic features of these groups, the alternation of convex and concave veins, and usually the change of convex ones into "inserted sectors." Such features are characteristic of these two recent groups and the related fossils, Triblosoba, Protodonata (in part), some Megasecoptera and evidently some Palæodictyoptera.

The study of the relation of the jugal areas to the remaining part of the wing lead me in another work (7) to the conclusion that the *Insecta Pterygota* probably separated during the Lower Carboniferous into several branches which went along different lines of evolution, the Paleoptera (Palæodictyoptera, Megasecoptera, Agnatha, with their Carboniferous relatives) and the Neoptera (the remainder of the Pterygota, which at rest fold their wings roof-like over their abdomens). My study of the venation and the tracheation of the wings of may-flies and dragon-flies proves this conclusion, because according to the wings both these groups are similar in many ways to the Dictyoneuridæ, Triblosoba, and the typical members of the Paleoptera.

In conclusion, I would like to discuss one more question. How can one explain that out of the once rich and diverse group of Paleoptera, there are now existing only the Agnatha and the Odonata, the other groups having died out? I think that in a discussion of this question we should not forget the structure of such an important organ as the wing.

Of course the wings of recent dragon-flies are much more perfect than those of their remote ancestors, which were like the Dictyoneuridæ. They have lost most of those veins of their ancestors which were unnecessary from a

mechanical point of view (among the even the main branches of M and Cu); they have changed their form (may-flies) and have acquired (dragon-flies) such important mechanical structures as the triangle and the parts adjacent to it, that they have in general become greatly mechanized; but by this means we hardly can explain the persistence of these two groups, because the wings of many extinct groups had also attained that mechanical perfection, particularly the Megaseoptera, Protodonata, and many groups and families of the Palæodictyoptera. The Megaseoptera, as well as the other groups mentioned, advanced very far, but nevertheless died out early. Evidently all this explanation is insufficient and something else is needed. Comparing the wings of may-flies and dragon-flies with the wings of the most primitive forms, e. g., Dictyoneuridæ from one side, and from the other side the Megaseoptera, Protodonata and more specialized Palæodictyoptera, we find, between the one and the other, distinct differences. In the Megaseoptera the venation is so much reduced that their wings resemble those of the Dictyoneuridæ only slightly.

In the Protodonata the number of longitudinal veins, on the contrary, has increased greatly, but the relative dimensions of the systems of Rs, M and Cu, and the distribution of their branches have greatly departed from that which we have seen in the Dictyoneuridæ. Similar changes in dimension and distribution of branches are encountered in many Palæodictyoptera. Dragon-flies (especially Anisoptera) and may-flies, on the contrary, differ in that, disregarding the various specializations, they preserved the original relative dimensions of the systems of the main veins and the distribution of branches (especially Rs!). The Anisoptera preserved their primitive form of wing. Such preservation of the fundamental primitive features was the reason why the specialization of the wings of dragon-flies and may-flies did not become fatal for them, as in the case of the former groups. *A too rapid specialization, with the loss of the original primitive features, as we have in the Megaseoptera, Protodonata, etc., inevitably narrows greatly the potentiality of further evolutionary modifications, and leads such groups to an end of development and*

*consequently to extinction.*

And so this study of the venation of the two recent orders, the Agnatha and the Odonata, which to my mind represent the branches which separated early from the more primitive forms of the very similar Dictyoneuridæ, and which have nothing in common with the Neuroptera and Plectoptera<sup>16</sup>, leads me to the conclusion that such characteristic features of the venation and the distribution of veins (in particular RS, partly M) of the Dictyoneuridæ were preserved better in the dragon-flies and may-flies than in many Palæodictyoptera or Megasecoptera, in which the venation was too specialized or too reduced. May, 1923.

P. S. My work was already in the press of the Russian Entomological Review when the July number of Psyche (30:1923, nos. 3-4) appeared, with an article by Aug. Lameere on "The Wing Veins of Insects." In this small but very valuable article, the author discusses chiefly the venation of the Palæodictyoptera, the dragon-flies and the may-flies, and in many respects comes to the very same conclusion on the question of the interpretation of the venation as I have.

In the treatment of RS in the dragon-flies and the may-flies we agree perfectly, aside from terminology. According to Lameere, also, the media of may-flies corresponds to the posterior branch (our MP), in Triblosoba, etc., and the media of the dragon-flies according to the author is MA (my terminology). From a comparison of the Protodonata, I now entirely share this interpretation, according to which the dragon-flies lost MP. In the treatment of the cubitus we do not agree in everything, because the assertion of Lameere that the may-flies, as well as the dragon-flies, have lost CuA, is to my mind not entirely proven. I will not discuss here the venation of the other groups, and will note only that the conception of the author that there is a close relation between the Hemiptera and the Palæodictyoptera appears to me unlikely. According to my understanding of the venation of Eugeron, it is constructed entirely after the type of the Palæodictyoptera, and is far from the type

<sup>16</sup> The Plecoptera have to be included according to my understanding into the super-order Orthopteroidea. A similar view has been taken by Lameere (1917).

of the Hemiptera. Eugereon, together with several other forms, represents only one on the branches of the Palæodictyoptera, and one can hardly connect it with the Hemiptera, which represents an entirely different trunk and must be referred to my group Neoptera; the latter separated very early from the division Paleoptera, to which one should assign Eugeron Dorhn. To all these questions I hope to return. Fall, 1924.

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## EXPLANATION OF FIGURES

- Fig. 1. Wing (hind?) of *Polioptenus elegans* Goldenberg.  
 Fig. 2. Fore wing of *Eumecoptera laxa* Gold.  
 Fig. 3. Wing of *Triplosoba pulchella* Brongn.  
 Fig. 4. Wings of *Hexagenia bilineata* Say.  
 Fig. 5. Fore wing of *Gomphus descriptus*.  
 Fig. 6. Basal part of hind wing of *Heterophlebia dislocata* Brodie and Westw.  
 Fig. 7. Base of hind wing of *Phylopetalia apicalis* Selys.  
 Fig. 8. Wing of *Protomyrmeleon brunonis* Geintz.  
 Fig. 9. Tracheation of wing of nymph of *Lestes rectangularis* Say.  
 Fig. 10. Hind wing of *Palingenia longicauda* Oliv., after Eaton (5).  
 Fig. 11. Tracheation of the *anlage* of the fore wing in the adult nymph of a member of the Hexagenioidea Ulm. (original).  
 Fig. 12. Anormalous tracheation in the hind wing *anlage* of a nymph of *Æschna* sp. (original).  
 Figures 1, 2, 3, 6, and 8 after Handlirsch (6); Fig. 4 after Needham (8); Figs. 5, 7, and 9 after Needham (10).